A SYSTEM OF GROUP NAMES FOR SOME TERTIARY POLLEN

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ABSTRACT. Analysis of the literature has shown that the use of form taxa to describe tricolpate and tricolporate pollen grains from the European Tertiary has little stratigraphic or botanical value. An alternative methodology for investigating Tertiary pollen involves two stages in the process of observation and description. One of these, the first phase, is dealt with in this paper, and involves assigning pollen to a group by means of a simply defined grid; this enables easy identification of all possible types. The second phase demands the use of sophisticated techniques for observation and comparison so as to establish details of botanical affinity and biostratigraphic correlation. The first-phase procedure is demonstrated by reference to pollen assemblages from three deposits in the western part of the British Isles.

THE rapid increase in the number of publications on pre-Pleistocene palynology over the past twenty-five years has produced an excessive number of described taxa, and this has created many taxonomic problems (Kremp and Methvin 1968). This fundamental difficulty is clearly evident in a study of a number of European Tertiary pollen and spore assemblages (text-fig. 2) in which large numbers of tricolpate and tricolporate pollen are encountered. These types of pollen are commonly present in many European Tertiary assemblages and have been regularly described over the past 40 years. Nevertheless, their identification is still very difficult and their stratigraphic and botanical usefulness is increasingly regarded as being negligible.

This paper is an attempt to review that information from the literature which might have continuing importance to aspects of stratigraphy and evolution, and to illustrate the use of such knowledge in describing assemblages from three Tertiary deposits. The new method of analysis which is used involves the designation of a small number of groups of pollen which are very simply defined and which we propose as alternatives to binomial nomenclature. Since these groups are defined by two characters (polar length and surface sculpture) which are usually available in the records of established taxa, we have been able to analyse the literature to show that the groups have as much stratigraphic value as the original binomial taxa. This work only applies to fossil pollen which has been compressed perpendicular to the polar axis—equatorially flattened forms of tricolpate and tricolporate pollen have only rarely been described in the European Tertiary and usually occur in small quantities.

In the past, palynologists have used very different levels of detail to establish definitions of new form genera and species, and techniques of preparation, sampling, and illustration have also varied considerably in quality and detail. One consequence of this variation is that, for an over-all comparison from the literature, the number of characters that can be used is limited by the minimum detail available in any one major published work. We propose that, for the purposes of the first phase in the analysis, which involves the initial identification and comparison of pollen from different Tertiary assemblages, very simple uncontroversial characters should be used. This can be achieved by the use of a simple method of group identification within

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a grid (Tables 1 and 2, rather than by the use of form taxa. This method of identification involves only ten primary first-phase groups, which replace about 115 form species of tricolporate pollen that have been described in the literature. Although in this paper we are advocating a rather simple systematic treatment of these pollen types (our 'first phase') it is clear that on a long-term basis a more searching and elaborate systematic treatment may yield more refined stratigraphic and botanical data (our 'second phase'). This second phase of operation demands a very detailed level of study, with the use of the electron microscope for examination and comparison with other fossil material and with modern equivalents, as well as the use of other advanced techniques such as computer analysis (Germeraad and Muller 1970). When it is necessary to create new form species or biorecords (Hughes and Moody-Stuart 1969) as much information as possible must be provided so as to define the taxa precisely.

SOME PROBLEMS OF NOMENCLATURE IN TERTIARY PALYNOLOGY

Though the concept of the form taxon is useful for Tertiary macrofossils, the experience of the last 40 years of palynology has shown that it has a far more limited value if applied to Tertiary pollen and spores. There are two major reasons for this. During the Tertiary, angiosperm evolution was progressing rapidly, so that large numbers of species must have existed during that time. There are more than 250 000 species of angiosperms in existence today (Sporne 1974), and many more must have existed over the 63 million years of the Tertiary period. Such a diversity over such a length of time is found in few other groups. Given the diversity, it would not have been surprising if those attempting to classify various types of Tertiary pollen had found this a difficult task, even if these pollen types had exhibited a large number of characteristics on which their classification could be based. However, many commonly occurring types of Tertiary pollen, particularly tricolpate and tricolporate ones, show comparatively few characters; that these show little variation makes the problem more difficult. Indeed, much of the confusion about fossil tricolpate and tricolporate pollen types is due to the well-known controversies about pollen morphology (Kremp 1965) in which authors interpret the same morphographic terms in different ways. In addition, problems of morphological interpretation of light microscope studies abound, though many of these can now be resolved by the use of the electron microscope.

Some of these difficulties were recognized by Erdtman (1947, 1948) who proposed the formation of an informal system of identification based on 'sporomorphs'—names which describe the major morphological types of pollen without the constraints of the International Code of Botanical Nomenclature. Though adopted by Cookson (1947), this system has been criticized for the confusion that it creates through similarity with the formal methods (Schopf 1949) and for its disregard of any association with modern botanical affinity (Traverse 1955). Most European palynologists have therefore continued to use the formal binomial (though without paying much attention to the nature of the type specimens), perhaps mainly because it is easy to use the form generic names created by Thomson and Pflug (1953) as these are defined in broad and simple terms. Claims of their affinity to genera or families that are defined with extant plants must still be treated with extreme caution. Brown (1957), in a review of European Tertiary pollen studies, urges the creation of a system of 'classification' based on the pollen morphology, in order to facilitate the rapid determination of individual grains within a particular assemblage. Others have chosen to make their identifications outside the rules of the Code by using informal group names which lack any precise definition and are usually based on a set of poor photographs with little or no verbal description (Krutzsch 1958; Sontag 1966; Kedves 1967). Since the time of Traverse's (1955) review of methods of nomenclature in Tertiary palynology, the trend has been to use one of three methods to describe the components of pollen and spore assemblages: form taxa, modern taxa, or form groups.

The use of form taxa

Since the rejection of Robert Potonié's form genus *Pollenites* (Potonié 1958) the subsequent confusion has brought about several variations on this formal system of naming and division. Most contemporary European Tertiary palynologists follow Thomson and Pflug's (1953) use of form genera such as *Tricolporopollenites* Thomson and Pflug (tricolporate pollen), *Tricolpopollenites* Thomson and Pflug (all tricolpate pollen) and *Subtriporopollenites* Thomson and Pflug (all pollen with three simple pores, all or in part subequatorial). These form genera are defined very clearly and simply, and the chief criticism of their use has been their lack of emphasis on possible relationships to extant plant taxa (Traverse 1955). This has not prevented many European palynologists since 1953 from using these names, though a few (e.g. Krutzsch 1961, 1970) have split some of the largest categories. The principle is the same in all cases: a form genus is defined simply on major morphological characteristics, and a form species is usually based on specimens from one assemblage, the amount of detailed description varying according to the judgement of the author. This method of citation of form genera and form species suffers from four difficulties. (1) There is often little or no stratigraphic restriction on the range of the major form taxa within the European Tertiary. Indeed, most have very long ranges and some extend even to the Palaeozoic. Few, if any, Tertiary palynomorphs have a well-understood age range. (2) There are problems connected with different authors' value-judgements on the amount of detail necessary for diagnosis, as well as with variations in the interpretation of characters and in preparation and preservation. Hughes and Moody-Stuart (1967) have discussed some of these difficulties when proposing that more than 100 specimens be available prior to the erection of a new form species or biorecord. (3) When a new assemblage is studied it is common to find that some specimens cannot readily be interpreted as belonging to form species already known from other assemblages. This difficulty can be overcome in one of two ways. First, these specimens can be referred to a new form species, though only rarely do other workers refer their specimens to these taxa. Secondly, they may be tentatively referred to an existing form taxon by the use of devices such as *cf.* B or *cf.* C for form species (Hughes and Moody-Stuart 1967) or *Genus* sp. A for form genera (Manum 1962; Machin 1971). (4) The small amount of comparison with modern forms that is recorded within the literature provides few opportunities for reliable assignment to categories of living plants. Very little is known of the detailed morphology from extant species of angiosperms, though a few species are well understood.

Palynological studies can contribute to the solution of two types of problem—stratigraphic and phyletic. Because of the difficulties described above, the interpretation of common types of European Tertiary pollen in terms of form taxa has thrown little light on either of these problems, with the exception of the few forms that are easy to identify because of some morphological peculiarity. This is confirmed by our own analysis and use of Thomson and Pflug's (1953) form species (see below).

The use of modern taxa

In the European literature, a few authors have used modern generic names to describe angiosperm pollen from Eocene, Oligocene, or Miocene deposits. Macko (1957), Simpson (1961), and Machin (1971) are the most prominent examples, but both the limited modern pollen reference collections available to them, and the lack of advanced facilities for observation, make it impossible for them to have made substantial detailed comparisons. Many macrofossils occurring within European Tertiary deposits have been identified as belonging to modern genera, but few palynologists other than Machin have been willing to use this knowledge to support a similar identification of the pollen from the same deposit. Using such indications, pollen identification is occasionally possible to the generic level, but not to the specific level. Indeed, many evolutionary botanists (Stebbins 1950; Takhtajan 1969) argue that few modern angiosperm species existed more than 10 million years ago, and few modern genera more than 35 million years ago. Because patterns of plant dispersal in North America were so different from those in Europe, the practice of American workers such as Traverse (1955) and Leopold and Macginitie (1972) in commonly citing modern genera to identify Oligocene pollen is more acceptable there (Wolfe and Hopkins 1967). However, the assignments are rarely confirmed by detailed comparisons with their modern equivalents as well as with fossil material from Europe.

The use of form groups

Krutzsch (1958, 1970), Sontag (1966), and Kedves (1967) have created more than 200 morphological categories that they call form groups, and which may be used in stratigraphic correlation: most of them are shown to have clearly restricted age ranges. There are two major weaknesses in this method of description. First, none of the authors has produced anything more than a photograph to define each group, and their scientific value is therefore very limited. Other workers cannot assign their specimens to these form groups solely from comparison with these published pictures. Secondly, the range charts are based on material that is limited both geographically and stratigraphically. As with the use of form taxa, the more these stratigraphic limits are tested, the more they are extended. For instance, Krutzsch's more recent publication (1970) provides a stratigraphic revision to some of the form groups which extends their age range.

PROPOSAL FOR A TWO-PHASE APPROACH

The future development of Tertiary palynology is likely to be impeded by the existence of these three conflicting systems of naming. If they persist, the literature will become increasingly swamped with unmanageable numbers of new taxa defined at different levels of detail, whilst ever more extended stratigraphic ranges will still further reduce their usefulness. Our first-phase procedure concerns problems associated with preliminary investigation, particularly when different assemblages are being compared. It is here that the existing literature is useful, largely in establishing the limits of the range of morphological variation in the major types of pollen. Our concept of group identification uses existing knowledge of this to set up grids based on the combination of two variables, both of which have wide ranges of variation. Consequently, any pollen within these ranges will fall into one group within the grid. Although the method is applied here only to the identification of tricolporate and tricolpate pollen grains that are compressed in the polar axial plane, other grids can be devised to designate other types of pollen (e.g. tricolpate and tricolporate pollen flattened in the equatorial plane—a very small amount of this kind of pollen is found in the European Tertiary; triporate pollen, etc.). These different grids can vary in the characters used for definition of the co-ordinates as well as in the extent of any size limits that might be involved. Differently defined grids can be devised for different assemblages, according to the kinds of pollen within each major type that occurs. For instance, the tricolpate pollen that occurs at one locality may be suitably described with psilate, scabrate, and baculate sculpturing characters as one co-ordinate, and polar length ranging from 0 to 25 μm and from 15 to 40 μm as the other. Tricolpate pollen from another locality may have the same types of sculpturing but different size limits of polar length, 0–20 μm and 20–40 μm.

Our second-phase procedure would consist of a very precise level of examination using as many advanced techniques as possible. So far, work to this level of detail has not been attempted in Europe, and little can therefore be said of its potential. Hughes (1970) has discussed the way in which such precise work can help with correlations within the Cretaceous. Also, some of the work of Krutzsch (1961) has achieved a high level of detailed description from light-microscope observations, together with interpretations giving correlation with other pollen-bearing deposits in East Germany. But there is no doubt that other structural detail can be obtained more accurately from the electron microscope, and that this can then be used for correlation within the whole of the European province.

The first-phase groups have been devised from a knowledge of the extent of variation within tricolpate and tricolporate pollen of the European Tertiary. Their designation here arose from our confrontation with the very large numbers of pollen from these types which occur in assemblages throughout the European Tertiary. The majority of dicotyledon pollen is of the tricolpate or tricolporate type, and our quantitative analysis of palynomorphs from many European Tertiary assemblages shows that often as much as 80% of the pollen present is of these types. Placing such pollen in existing form taxa is difficult and provides little useful information. Thomson and Pflug (1953) identified eleven form species of tricolpate pollen and thirty-nine tricolporate species from the German Tertiary, and these names are those most commonly used in subsequent studies (see Appendix 1). Our review of work reported in sixteen papers (A–P in Appendix 1) on European Tertiary palynology published since then shows two important tendencies. First, those taxa that have been recorded more than once since 1953 have had their stratigraphic range extended to cover most of the Tertiary. Secondly, those taxa with a restricted range have rarely been referred to by other authors; we believe that this is due to the limitations of the original descriptions of these taxa and does not imply that their geographic and stratigraphic ranges are significantly restricted. Since 1953, some workers have proposed new form species of both tricolpate and tricolporate pollen, though few of these have ever been recognized in the published work of others. Our conclusion from this review, therefore, is that no single existing taxon of tricolpate or tricolporate Tertiary pollen contributes to the solution of stratigraphic problems. It is also widely accepted that the determination of the botanical affinities of these types of pollen cannot be made (Krutzsch 1970).

It was against this background that we began to search for a simpler way of designating the tricolpate and tricolporate pollen from the European Tertiary. There is little value in making dubious identifications if the resulting names have little significance, and a simple method of avoiding such ambiguity is therefore preferable. The only characteristics that are regularly used within the literature to identify these pollen are polar length and sculpturing type and, under certain clearly defined limits, both these features can easily be recognized. Polar length may vary with particular preservation and preparation effects, but not significantly. The polar length is not changed significantly by preservation except when the pollen grain has been flattened equatorially. This type of compression is rare for prolate and otherwise elongate forms of tricolpate and tricolporate pollen. In the European Tertiary it is generally confined to *Tricolporopollenites kruschi accessorius* (Potonié 1934) Thomson and Pflug 1953, *T. kruschi analepticus* (Potonié 1934) Thomson and Pflug 1953, *T. iliacus* (Potonié 1931) Thomson and Pflug 1953, and small scabrate tricolpate pollen grains. If such palynomorphs are encountered in significant quantity, it may be necessary to define a grid system to accommodate them. Thomson and Pflug (1953) erected the Turma Brevaxones to accommodate equatorially flattened pollen grains, but did not include the genera *Tricolpopollenites* or *Tricolporopollenites*, which are strictly referable to the Turma Longaxones.

In the case of polar length, the limits of definition of the first-phase groups are described on the basis of practical convenience for the types studied, so as to provide the least difficulty in allocating individual specimens to the groups (Tables 1 and 2). Different assemblages of tricolpate and tricolporate pollen may therefore require different limits of definition. In the case of the second characteristic commonly available, the type of surface sculpturing, the definitions of the different types used follow those of Faegri and Iversen (1964) and are explained in text-fig. 1. If necessary, other columns can be added to accommodate pollen with different types of sculpture (e.g. granulate). Specimens with two types of surface sculpture, such as when that at the poles differs from that at the equator, can be allocated to two combined groups, e.g. 3C: SCA 1–PSI 1.

This system, using a combination of polar length and exine sculpture, is designed to accommodate tricolpate and tricolporate pollen types flattened along the polar

TABLE 1. Grid for first-phase groups of tricolpate in the European Tertiary. The four types of surface sculpture are defined in text-fig. 1. Existing form taxa can be allocated to these groups as listed in the text.

<table>
<tr><td>echinate</td><td colspan="3">ECH 1</td></tr>
<tr><td>baculate</td><td>BAC 1</td><td colspan="2">BAC 2</td></tr>
<tr><td>scabrate</td><td>SCA 1</td><td>SCA 2</td><td>SCA 3</td></tr>
<tr><td>psilate</td><td>PSI 1</td><td colspan="2">PSI 2</td></tr>
<tr><td></td><td>0–30</td><td>30–50</td><td>50–80</td></tr>
</table>

polar length – microns

TABLE 2. Grid for first-phase groups of tricolporate pollen in the European Tertiary. The five types of surface sculpture are defined in text-fig. 1. Existing form taxa can be allocated to these groups as listed in the text.

<table>
<tr><td>reticulate</td><td>RET 1</td><td>RET 2</td><td>RET 3</td></tr>
<tr><td>clavate</td><td colspan="3">CLA 1</td></tr>
<tr><td>baculate</td><td>BAC 1</td><td colspan="2">BAC 2</td></tr>
<tr><td>scabrate</td><td>SCA 1</td><td colspan="2">SCA 2</td></tr>
<tr><td>psilate</td><td>PSI 1</td><td colspan="2">PSI 2</td></tr>
<tr><td></td><td>0–35</td><td>35–55</td><td>55–80</td></tr>
</table>

polar length – microns

axis. First stage grids based on other characters will be needed to accommodate other types of pollen that may be particularly abundant and difficult to assign to conventional form taxa. For instance, pollen belonging to *Triatriopollenites*, *Triporopollenites*, *Trivestibulopollenites*, *Subtriporopollenites*, *Intratriporopollenites*, and *Porocolpopollenites* have been assigned to sixty-five form species by Thomson and Pflug (1953). Trial and error has shown that the most suitable characters for grid definition of these pollen are the type of aperture and the grain diameter.

Grids constructed on the basis of the two characters polar length and exine sculpture have provided eight groups (Table 1) into which the existing tricolpate pollen form genera can be allocated, as follows:

3C: PSI 1	*Tricolpopollenites liblarensis liblarensis*	Thomson and Pflug 1953
	T. liblarensis fallax	Thomson and Pflug 1953
3C: PSI 2	*Pollenites parmularius*	Potonié 1934
3C: SCA 1	*Tricolpopollenites microhenrici intragranulatus*	Thomson and Pflug 1953
	T. microhenrici intrabaculatus	Thomson and Pflug 1953
	T. densus	Thomson and Pflug 1953
3C: SCA 2	*T. asper*	Thomson and Pflug 1953
	T. henrici	Thomson and Pflug 1953
	T. microstriatus	Cavagnetto 1970
	T. cavernoides	Cavagnetto 1970
3C: SCA 3	*Pollenites confinis pudicus*	Potonié 1934
	Tricolpopollenites pudicus	Thomson and Pflug 1953
3C: BAC 1	*T. retiformis*	Thomson and Pflug 1953
3C: BAC 2	*T. pseudoeuphorii*	Thomson and Pflug 1953
3C: ECH 1	*Pollenites spinosus*	Potonié 1931

Similarly, the two characters provide ten groups (Table 2) into which the existing tricolporate pollen form taxa can be allocated, as follows:

3CP: PSI 1 *Pollenites facetus*, *P. ansatus*, *P. megaexactus*, *P. exactus minus*, *P. doliiformis*, *P. oviformis*, *P. lembus*, *P. fusus*, *P. cingulum fusus*, and *P. cingulum ovalis*, Potonié 1931. *P. exactus*, *P. quisqualis*, *P. quisqualis pusillus*, and *P. cingulum brühlensis*, Potonié 1934. *Tricolporopollenites cingulum fusus*, *T. cingulum pusillus*, *T. cingulum oviformis*, *T. megaexactus brühlensis*, and *T. megaexactus exactus*, Thomson and Pflug 1953. *T. laevigatus* and *T. mansfieldensis*, Krutzsch 1969.

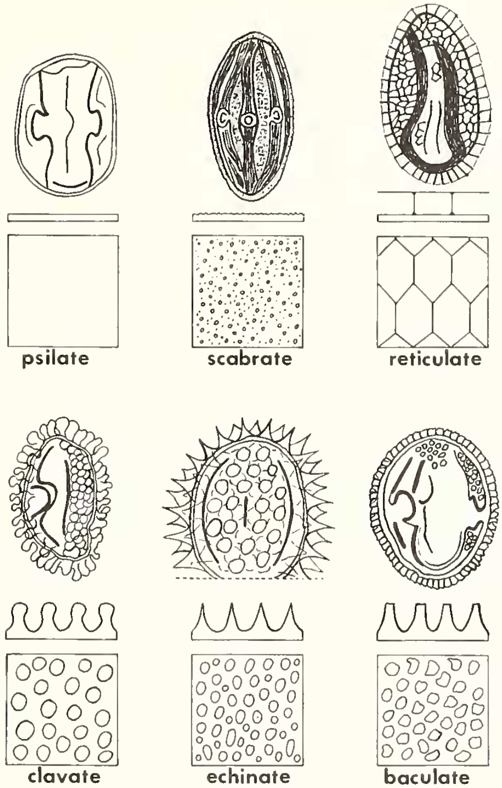
3CP: PSI 2 *Pollenites manifestus* and *P. inornatus*, Potonié 1931. *P. manifestus multiexituum*, Potonié 1934. *Tricolporopollenites eschweilerensis*, Thomson and Pflug 1953.

3CP: SCA 1 *Pollenites caseolus*, *P. pompeckji*, *P. pseudocingulum*, *P. pseudocingulum granulatum*, *P. thomsi*, *P. megagertrudae*, *P. fraudulentus*, *P. interruptus*, *P. ventosus*, *P. inornatus*, *P. pulvinus*, *P. navicula*, *P. dolium solum*, *P. dolium megaventiosum*, *P. dolium clarum*, *P. rauffi*, *P. laesus*, *P. pseudolaesus*, and *P. pseudocruciatus*, Potonié 1931. *P. selectus*, *P. pseudocingulum navicula*, *P. pseudocingulum rauffi*, *P. abbreviatus*, *P. gertrudae propius*, *P. pseudocruciatus pantherinus*, *P. orthoaesus*, *P. kruschi analepticus*, *P. kruschi scutellatus*, *P. kruschi dispar*, and *P. kruschi accessorius*, Potonié 1934. *P. laesus microlaesus*, Potonié and Venitz 1934. *Tricolporopollenites kruschi contortus*, *T. pseudocingulum*, *T. steinensis*, *T. pacatus*, and *T. satzveyensis*, Thomson and Pflug 1953. *T. eislebensis*, Krutzsch 1961. *T. singularis*, *T. stanleyi*, and *T. globosus*, Cavagnetto 1970.

3CP: SCA 2 *Pollenites megadolium digitatus*, *P. megadolium sinuatus*, and *P. orthoaesus lasius*, Potonié 1934. *Tricolporopollenites porasper*, *T. kruschi rodderensis*, *T. donatus*, *T. pseudocruciatus*, and *T. lasius*, Thomson and Pflug 1953.

3CP: BAC 1 *Pollenites euphorii* and *P. caroli*, Potonié 1931. *Tricolporopollenites microporitus* and *T. villensis*, Thomson and Pflug 1953. *Pollenites cingulum villensis* Potonié, Thomson, and Thiergart 1950. *Tricolporopollenites baculatus* Krutzsch 1961. *T. pseudoaceroides* Cavagnetto 1970.

3CP: BAC 2 *Pollenites edmundi* and *P. edmundi tenuis*, Potonié 1931. *Tricolporopollenites baculoferus*, *T. marcodurensis*, *T. wallensenensis*, *T. helmstedtensis*, and *T. borkenensis*, Thomson and Pflug 1953.



TEXT-FIG. 1. Definitions, after Faegri and Iversen (1964), of the terms used here to describe the surface sculpture of the pollen grains from some of the first phase-groups. For each type of sculpture there is a drawing of (*top*) the equatorial view of the pollen grain, (*middle*) the sectional view, and (*bottom*) the surface view.

PSILATE: surface even, or with pits no greater than 1 μm in diameter. Drawing of pollen from equatorial view is from group grid 3CP: PSI 1, ×2000.

SCABRATE: no dimension of surface sculpturing greater than 1 μm in diameter. Drawing of pollen from equatorial view is from group grid 3CP: SCA 2, ×1000.

RETICULATE: elements greater than 1 μm and forming a reticulum. Drawing of pollen from equatorial view is from group grid 3CP: RET 1, ×2000.

CLAVATE: upper end of sculpturing element thicker than the base, though the element is greater than 1 μm. Drawing of pollen from equatorial view is from group grid 3CP: CLA 1, ×1000.

ECHINATE: sculpturing elements greater than 1 μm in length and pointed at the tips. Drawing of pollen from equatorial view is from group grid 3C: ECH 1, ×2000.

BACULATE: upper end of sculpturing element not thicker than the base, though the element is greater than 1 μm. Drawing of pollen from equatorial view is from group grid 3CP: BAC 2, ×1000.

3CP: RET 1 *Pollenites petzoldti*, Potonié 1934. *Tricolporopollenites microreticulatus*, Thomson and Pflug 1953. *T. aceroides*, Krutzsch 1961. *T. striatoreticulatus*, Krutzsch 1962. *T. staresedloensis*, Krutzsch 1969.

3CP: RET 2 *Pollenites areolatus*, *P. ornatus*, *P. psoraleus*, and *P. grossularius*, Potonié 1934. *Tricolporopollenites sustmanni*, Thomson and Pflug 1953. *T. striatoides*, Krutzsch 1961. *T. eocenicus*, Krutzsch 1969.

3CP: RET 3 *Pollenites genuinus*, Potonié 1934.

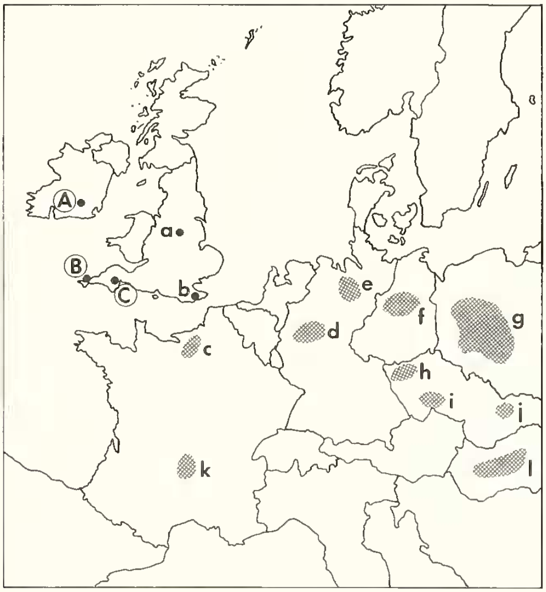
3CP: CLA 1 *Pollenites margaritatus* and *P. iliacus*, Potonié 1931. *P. propinquus*, Potonié 1934. *Tricolporopollenites iliacus major*, *T. iliacus medius*, *T. clavopolatus*, *T. margaritatus medius*, *T. margaritatus minor*, *T. margaritatus major*, and *T. coronatus*, Thomson and Pflug 1953. *T. mydloverensis*, Pacltova 1960. *T. ipilensis*, Pacltova 1966. *T. microiliacus*, Thomson and Pflug 1953. *T. vermiculatus*, Cavagnetto 1970.

APPLICATION OF THE FIRST-PHASE METHOD

We have applied this system to our investigations of the palynology of three Tertiary deposits in the western part of the British Isles to determine its practical usefulness. Plant-bearing clay at Ballymacadam (Co. Tipperary, Ireland), the Bovey Formation (Devonshire), and Saint Agnes (Cornwall) yield assemblages which contain more than 75% tricolpate and tricolporate pollen, compressed on their polar axis, in some parts of the sections. Due particularly to the presence of *Bohlensipollis hohli* Krutzsch, *Dicolpopollis kockeli* Pflanzl, and the many types of monocolpate palm-like pollen, each deposit is thought to be of an Oligocene age. Other than that they occur in very high proportions, the tricolpate and tricolporate pollen have not helped directly in determining the age of the deposits. Further details of the assemblages and their significance will be presented elsewhere. But the important issue here is that in all three assemblages the allocation of tricolpate and tricolporate pollen to the first-phase groups was quick and unequivocal in every case. The three assemblages are listed in Appendix 2, in which the tricolpate and tricolporate pollen is allocated to these first-phase groups and the remaining palynomorphs are allocated to established form taxa.

As well as it being an easier method of identification, so preventing different interpretations by different workers and speeding up the process of giving names in quantitative analysis, the method does have some stratigraphic importance. From the data presented in Appendix 1 as well as that from other work (Potonié 1931, 1934; Potonié and Venitz 1934; Potonié, Thomson, and Thiergart 1950; Thomson and Pflug 1953; Krutzsch 1961, 1962, and 1969) we have been able to calculate the occurrence of tricolpate and tricolporate pollen within the European Tertiary as documented in these twenty-four published articles (some of the most important works on European Tertiary palynology that have been published). This information is derived from borehole and surface samples from more than 100 localities, which come from the regions that are shaded in text-fig. 2. The age of the material represented extends from the Early Eocene to the Late Miocene, and each division of the stratigraphic scale (Harland *et al.* 1967) is represented, though not equally. The difference in representation of information at each point in the scale has been calculated and used to adjust each figure, so that each point of the scale is now represented equally by the data. For example, the Late Miocene is represented by three localities mentioned in the twenty-four articles, the Middle Oligocene by nine. The total number of records of pollen from the Late Miocene localities mentioned is multiplied by three (to give the same total of nine) to obtain equal representation.

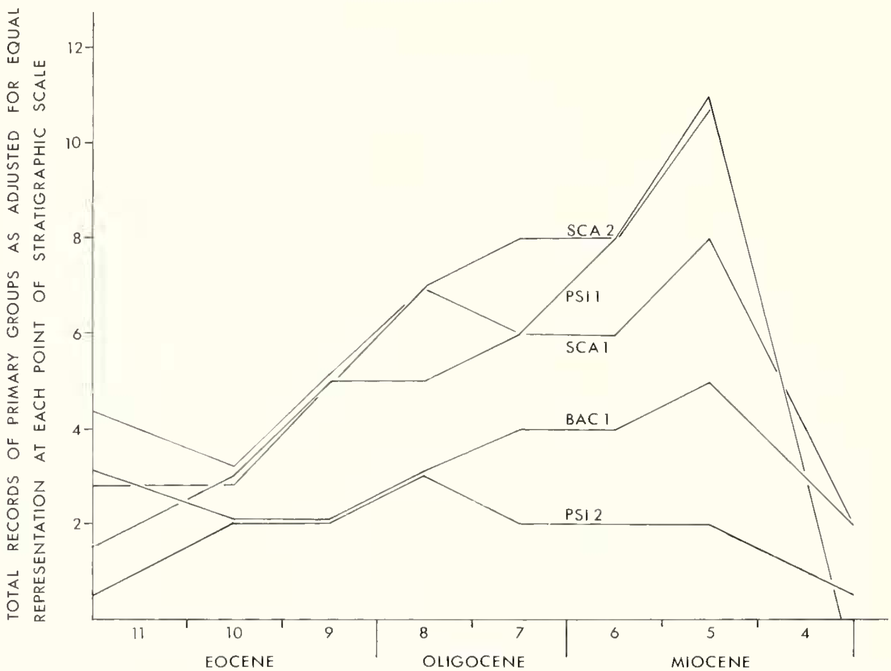
Palaeocene and Pliocene records have been omitted, due to the predominance of Mesozoic forms in the former and of modern genera in the latter. At the beginning of the Eocene and the end of the Miocene, major evolutionary events were taking place in land floras in response to environmental changes. Though there is some



TEXT-FIG. 2. *a–l*, regions of the European Tertiary localities which, according to the literature, have large proportions of tricolpate and tricolporate pollen. *a*, Brassington Formation, Derbyshire; *b*, Woolwich Formation, Kent; *c*, Paris basin; *d*, Rhine valley; *e*, Hamburg; *f*, Geiseltal; *g*, central Poland; *h*, Cheb basin, Czechoslovakia; *i*, southern Bohemia; *j*, Slovakia; *k*, Massif central; *l*, central Hungary. A–C, localities with pollen and spore assemblages identified here for the first time to test the system of group names that is proposed in this paper. A, Ballymacadam, County Tipperary; B, Saint Agnes, Cornwall; C, Bovey Formation, Devonshire.

continuity of forms across boundaries, the first-phase level of description is not based on accurate enough information to prove a continuity across these major evolutionary boundaries. It is thus preferable to include the age, as enumerated in Harland *et al.*'s stratigraphic scale (see Table 3), in any reference to a first-phase group. For example, 4. 3C: SCA 1 designates Late Miocene tricolpate pollen with scabrate sculpture and up to 30 μm in polar length, according to the particular grid definition of this paper.

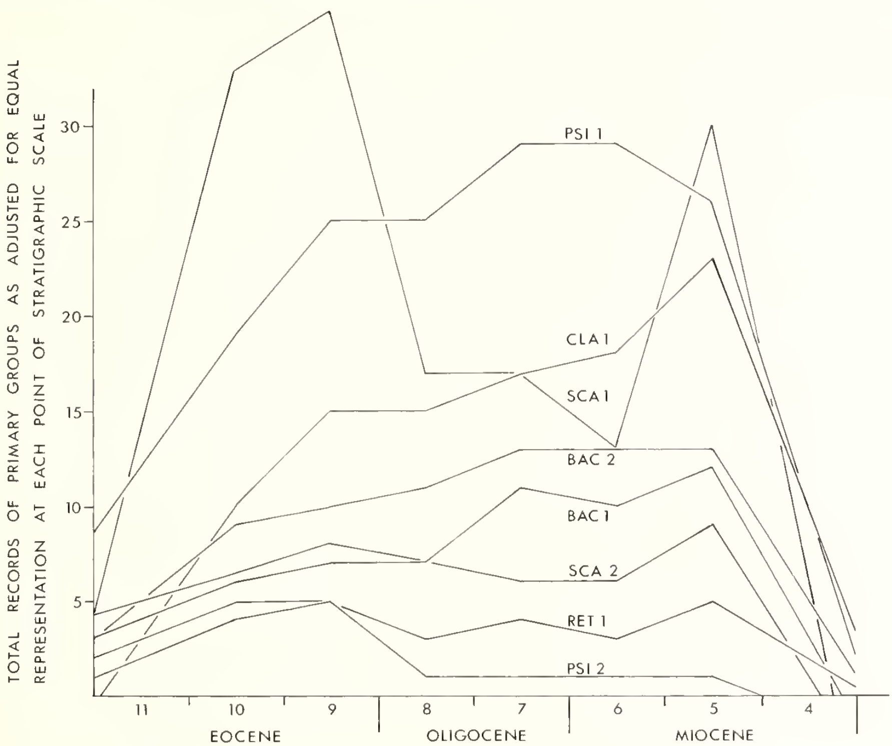
From our analysis of this data we have constructed graphs showing the change in occurrence of tricolpate first-phase groups (text-fig. 3) and of tricolporate first-phase groups (text-fig. 4); the total changes for all groups of each type are shown in text-fig. 5. Although it is important to emphasize the limitations of these calculations from such limited and controversial knowledge, a number of tentative conclusions can be made. It can be seen that some of the groups show particularly prominent peaks at



TEXT-FIG. 3. The twenty-four articles on Tertiary palynology referred to on page 568 contain data on the presence or absence of different form taxa of tricolpate and tricolporate pollen. This data has been translated into terms of first-phase groups by reference to the grids in Tables 1 and 2. These curves show the total number of times that some of the first-phase tricolpate groups are recorded as being present. The localities referred to in the twenty-four articles range in age from Early Eocene to Late Miocene, and the analysis therefore shows changes through this period. The figures on the horizontal axis refer to the stratigraphic scale used in Table 3 and Appendix 1.

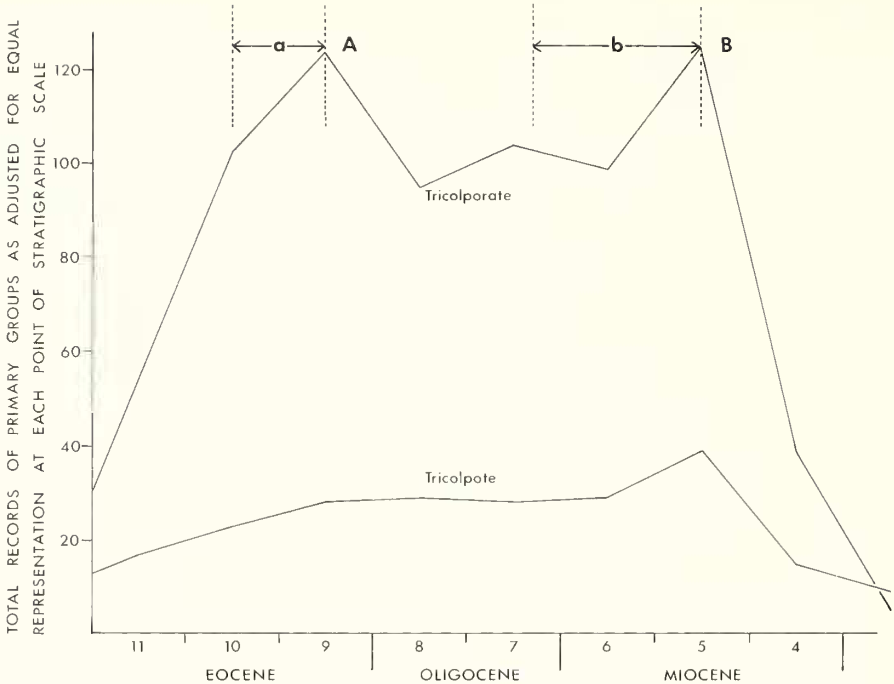
various points within the Tertiary (3C: PSI 1, SCA 1, SCA 2; 3CP: PSI 1, SCA 1, CLA 1). These show that, in the twenty-four selected articles, pollen from these groups is recorded more commonly from localities of these ages than of others; pollen from other groups have relatively small numbers of records in all the localities that are mentioned. In our three trial assemblages, for instance, there is a very high proportion of pollen from the two groups 3C: SCA 1 and 3C: PSI 2. Text-fig. 3 shows peaks for these groups in the Early–Middle Oligocene, which is commensurate with the age of the deposits as determined by other types of pollen.

Two other conclusions can be made from our analysis. The twenty-four articles contain data on the presence or absence of different form taxa of tricolpate and tricolporate pollen in more than 100 European localities. Text-fig. 5 shows results of our translations of this data into first-phase groups; the curves show the changes in the number of tricolpate groups and tricolporate groups throughout the Tertiary that are described in the data, as defined by our grids and as adjusted for stratigraphic misrepresentation. The tricolpate and tricolporate groups reach maximum peaks in the Middle Miocene localities and the tricolporate groups also reach a peak in the Late Eocene localities. Some kind of climatic cause seems likely for this, since a substantial reduction in annual mean temperature is thought to have taken place at these



TEXT-FIG. 4. A similar analysis of data as that for text-fig. 3, but for tricolporate pollen.

times (Krutzsch 1967; Dorf 1969; Wolfe and Hopkins 1967). The second general conclusion involves the equally broad implications of the curves to our understanding of the rates of evolution of angiosperms within the Tertiary, which is related to climatic change as well as to other environmental factors. The analysis (Table 3) of the times of the first appearance of 102 form taxa of tricolporate pollen shows particularly high first appearances during the Late Oligocene and the Middle Eocene. Both these maxima occur just before the times of the maximum peaks of all tricolpate and tricolporate pollen (text-fig. 5A, B). The two resulting intervals near the Eocene–Oligocene (text-fig. 5A) and the Oligocene–Miocene (text-fig. 5B) boundaries represent those periods of time when the plants producing these fossil pollen grains were no



TEXT-FIG. 5. Graph showing the number of times that pollen from all tricolpate and tricolporate first-phase groups have been recorded from the more than 100 localities described in the twenty-four articles referred to on page 568. Peaks A and B may be due to some climatic cause, whilst *a* and *b* represent the time intervals between the first occurrence of some form taxa (Table 3) and these peaks.

doubt becoming established, evolutionarily and ecologically. Such short periods of intense evolutionary activity have been discussed in quite different contexts by Ager (1973). The climatic deterioration that is thought to have followed each climax produced rapid changes in the flora, and this is reflected in the number of form taxa and first-phase groups that are recorded.

TABLE 3. The times of the first appearance of 102 form taxa of tricolporate pollen during the European Tertiary. The data is obtained from the sources listed in the legend to Appendix 1.

Division of the stratigraphic scale	Age	Number of taxa making their first appearance
Harland *et al.* 1967		
3	Pliocene	1
4	Late Miocene	0
5	Middle Miocene	2
6	Early Miocene	0
7	Late Oligocene	15
8	Lower to Middle Oligocene	4
9	Late Eocene	0
10	Middle Eocene	60
11	Early Eocene	20

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APPENDIX 1

The sources from which the original ranges of Thomson and Pflug's (1953) form species of tricolpate and tricolporate pollen have been revised. For each form species, details are given of: the phase-one group to which it is allocated; the original range as cited in Thomson and Pflug (1953) expressed in terms of the stratigraphic scale of Harland *et al.* (1967) (see Table 3); the occurrences recorded in sixteen articles (A–P, see below) published since 1953 ((+) denotes that details of the sub-form-species are not recorded in the literature); and the stratigraphic range as revised by these references. A, Pacltova 1963; B, Boulter 1971; C, Mazancova 1962; D, Ziembinska-Tworzydlo 1974; E, Neuy-Stoltz 1958; F, Mamczar 1960; G, von der Brelie 1968; H, Pacltova 1960; I, Doktorowicz-Hrebnicka 1957*b*; J, Doktorowicz-Hrebnicka 1957*a*; K, Pacltova 1966; L, Chateauneuf 1972; M, Pflanzl 1956; N, Grabowska 1965; O, Kedves 1969; P, Cavagnetto 1970.

	Group	1953 Range	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Revised range
Tricolpopollenites																			
pudicus	3C: SCA 3	10–11				+										+			5–11
henrici	SCA 2	5–8	+		+	+	+	+	+	+	+	+	+	+	+	+	+		3–11
asper	SCA 2	3–11			+		+			+					+	+	+		3–11
densus	SCA 1	8–11							+						+	+		+	5–11
microhenrici	SCA 1	4–11	+	+	+	+	+	+	+	+	+		+		+	+	+	+	3–11
liblarensis liblarensis	PSI 1	4–8		+			+	+	+	+	+	+	+		+		+	+	3–11
liblarensis fallax	PSI 1	3–10					+	+	+	+		+			+	+			3–10
parmularius	PSI 2	5–11				+										+			4–11
retiformis	BAC 1	3–11		+		+	+		+	+			+			+	+	+	3–11
pseudoeuphorii	BAC 2	10–11														+	+		8–11
spinosus	ECH 1	7–11	+							+					+				3–11
Tricolporopollenites																			
dolium	3CP: SCA 1	5–8			+	+	+			+	+	+				+	+		4–11
villensis	BAC 1	5–10			+	+	+		+	+	+			+	+	+	+	+	4–11
pacatus	SCA 1	8–10					+										+		5–11
pseudocingulum	SCA 1	8–10	+	+	+	+	+	+	+	+			+		+	+	+		3–11
cingulum fusus	PSI 1	8–10			+	+	+			+		(+)	+	(+)	+	+	+	(+)	4–11
cingulum pusillus	PSI 1	5–11			+	+			+	+	+		+		+	+	+		4–11
cingulum oviformis	PSI 1	8–10			+	+				+			+			+	+		4–11
megaexactus brühlensis	PSI 1	5–11			(+)	(+)	+	+	(+)	+	+	+	+		+	+	+	(+)	4–11
megaexactus exactus	PSI 1	5–11				+	+	+	+	+	+	+			+	+	+		4–11
steinensis	SCA 1	11														+	+		8–11
sustmanni	RET 2	5–8					+									+			5–8
edmundi	BAC 2	5–10		+	+	+	+	+	+	+	+	+	+	+	+	+	+		3–11
euphorii	BAC 1	5–11			+	+	+	+	+	+	+	+		+	+		+		4–11
borkenensis	BAC 2	5–10																	5–10
eschweilerensis	PSI 2	5–11															+	+	5–11
helmstedtensis	BAC 2	8–10																	8–10
wallensenensis	BAC 2	3	+		+	+											+		3–11
marcodurensis	BAC 2	5–8				+	+						+			+	+		4–11
satzveyensis	SCA 1	11				+				+						+		+	4–11

kruschi analepticus	SCA 1	5–11		+	(+)	(+)			+					+	(+)	+	(+)	4–11
kruschi accessorius	SCA 1	5–10												+		+		5–11
kruschi rodderensis	SCA 2	5–8							+									5–8
kruschi contortus	SCA 1	5–11														+		5–11
pseudocruciatus	SCA 2	5–8			+	+		+.	+					+	+			4–9
genuinus	RET 3	5–11		+					+		+			+	+	+		4–11
lasius	SCA 2	8–10														+		8–11
baculoferus	BAC 2	8–11														+		8–11
porasper	SCA 2	8–11				+			+					+		+		5–11
microreticulatus	RET 1	5–10		+		+		+	+			+		+		+		4–11
microporitus	BAC 1	8–10															+	8–11
iliacus major	CLA 1	5–10																5–10
iliacus medius	CLA 1	5–10	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	(+)	(+)	+		3–11
microiliacus	CLA 1	8–10				+			+					+	+			5–10
margaritatus major	CLA 1	5–10	(+)		(+)	(+)	(+)	(+)	(+)	(+)	(+)			(+)	(+)			3–10
margaritatus medius	CLA 1	3–10		+												+		3–11
margaritatus minor	CLA 1	3–10														+		3–11
clavopolatus	CLA 1	5–10																5–10
donatus	SCA 2	10–11														+		10–11

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henrici	SCA 2	5-8	+		+	+	+	+	+	+	·	+	+	+		+	+		3-11
asper	SCA 2	3-11			+		+			+					+	+	+		3-11
densus	SCA 1	8-11							+						+	+			5-11
microhenrici	SCA 1	4-11	+	+	+	+	+	+	+	+	+		+		+	+	+	+	3-11
liblarensis liblarensis	PSI 1	4-8		+			+	+	+	+	+	+	+		+		+	+	3-11
liblarensis fallax	PSI 1	3-10					+	+	+	+		+			+	+			3-10
parmularius	PSI 2	5-11				+										+			4-11
retiformis	BAC 1	3-11		+		+	+		+	+			+			+	+	+	3-11
pseudoeuphorii	BAC 2	10-11														+	+		8-11
spinosus	ECH 1	7-11	·							+					+				3-11
Tricolporopollenites																			
dolium	3CP· SCA 1	5-8			+	+	+			+	+	+				+	+		4-11
villensis	BAC 1	5-10			+	+	+		+	+	+			+	+	+	+	+	4-11
pacatus	SCA 1	8-10					+										+		5-11
pseudocingulum	SCA 1	8-10	+	+	+	+	+	+	+	+			+		+	+	+		3-11
cingulum fusus	PSI 1	8-10			+	+	+			+		(+)	+	(+)	+	+	+	(+)	4-11
cingulum pusillus	PSI 1	5-11			+	+			+	+	+		+		+	+	+		4-11
cingulum oviformis	PSI 1	8-10			+	+				+			+			+	+		4-11
megaexactus brühlensis	PSI 1	5-11			(+)	(+)	+	+	(+)	+	+	+	+		+	+	+	(+)	4-11
megaexactus exactus	PSI 1	5-11				+	+	+	+	+	-	+			+	+	+		4-11
steinensis	SCA 1	11														+	+		8-11
susinianus	RET 2	5-8					+									+			5-8
edmundi	BAC 2	5-10		+	+	+	+	+	+	+	+	+	+	+	+	+	+		3-11
euphorii	BAC 1	5-11			+	+	+	+	+	+	+	+		+	+		+		4-11
borkenensis	BAC 2	5-10																	5-10
eschweilerensis	PSI 2	5-11															+	+	5-11
helmstedtensis	BAC 2	8-10																	8-10
wallenseuensis	BAC 2	3			+	+											−		3-11
marcodurensis	BAC 2	5-8				+	+						+			+	+		4-11
satzveyensis	SCA 1	11				+				+						+		+	4-11
kruschi analepticus	SCA 1	5-11				(−)	(+)			+						(+)	+	( )	4-11
kruschi accessorius	SCA 1	5-10															+		5-11
kruschi rodderensis	SCA 2	5-8								+									5-8
kruschi contortus	SCA 1	5-11															+		5-11
pseudocruciatus	SCA 2	5-8				+	+		+	+					+	+			4-9
geminus	RET 3	5-11								+		+			+	+	+		4-11
lasius	SCA 2	8-10															+		8-11
baculoferus	BAC 2	8-11															+		8-11
porasper	SCA 2	8-11					+			+					+		+		5-11
microreticulatus	RET 1	5-10			+		+		+	−			+		+		+		4-11
microporitus	BAC 1	8-10																+	8-11
iliacus major	CLA 1	5-10																	5-10
iliacus medius	CLA 1	5-10		(+)	+	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	(+)	(+)	+		3-11
microiliacus	CLA 1	8-10					·			—					+	+			5-10
margaritatus major	CLA 1	5-10		(+)		(+)	(·)	(−)	(+)	(+)	(+)	(+)			(+)	(·)			3-10
margaritatus medius	CLA 1	3-10			+												+		3-11
margaritatus minor	CLA 1	3-10															+		3-11
clavopalatus	CLA 1	5-10																	5-10
donatus	SCA 2	10-11															+		10-11